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THE GENERA OF THE WOODY RANALES IN THE SOUTHEASTERN UNITED STATES

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THE TREATMENTS PRESENTED BELOW of the sixteen genera of seven woody ranalian families which occur in the southeastern United States have been prepared as part of a generic study of the seed plants of that area. This work has been undertaken as a joint project of the Gray Herbarium and the Arnold Arboretum and has been made possible through the interest and support of George R. Cooley and through a grant from the National Science Foundation. In view of the co-operation and interest others have shown in this undertaking it seems worth while to publish our treatments of at least some of the families in advance of the completed work. In this way some of the material brought together in the course of these studies will be made available, and we should hope to have constructive criticisms from other botanists as the work progresses. In attempting a generic treatment of the approximately 1300 genera of seed plants known to occur within the area bounded by and including North Carolina and Tennessee, on the north, and Arkansas and Louisiana, on the west, the objectives are toward a review and reorganization of familial and generic lines (often obscured in Small's Manual of the Southeastern Flora) and, especially, toward bringing together at least a part of the vast botanical literature which bears upon the plants of this rich area. The work is being done by taxonomists and is both taxonomic and floristic, but the approach, as well as the scope, is intended to be somewhat broader than is usual in a regional manual. The basic scheme is biological with the intent of including material from all branches of botany and of underscoring the biosystematic aspects of each genus and family, insofar as possible. In such an approach more problems may be raised than are solved but, in at least some instances, some of the difficulties which must be resolved before the plants of our area can be understood adequately become evident when the literature of a particular genus or family is brought together. Of course, with the existing information such a large goal is impossible for all genera (or even most) but a biological or biosystematic viewpoint is that which we are attempting to maintain throughout these studies.

The difficulties and weaknesses of this undertaking are apparent to no one more clearly than to those of us who have planned and worked on this project. More than a year and a half were spent on the tedious but basic chore of drawing together a file of more than 50,000 references arranged by families and genera which provided the starting point for the work. The large number of references and their wide distribution in the botanical literature of the world point up the almost incredible amount of information which is rather effectively "lost" to most botanists and even to authori-

ties on particular groups of plants. The amount of material published about some genera of plants (cf. Magnolia and Liriodendron) is very large, while that concerning others is so scattered and fragmentary that it seems almost impossible to retrace. The matters of locating references, attempting to deal with information from a number of fields, culling, and trying to synthesize in a few choice words the "essence" of the genus sometimes seems to be (and probably is) a nearly hopeless task. The degree of success undoubtedly varies considerably from one group to another, and both sins of omission and commission will be evident. However, the work is absorbing and it is difficult to set aside one group for another, leaving behind many unsolved problems. It is to be hoped that others may take an interest in some of these problems and that the notes and references included will prove to be useful to students and researchers. One thing is certain: there are enough botanical problems in the Southeastern flora to supply all possible workers for a long time to come. Although the general scheme being followed throughout this work will be apparent in the treatments below, a few explanatory comments will be apropos. It should be noted especially that the descriptions of families and genera are based mainly upon the species which occur in the southeastern United States and are not necessarily wholly applicable to those beyond this area. However, additional information which may provide a more balanced concept of the genus may sometimes be included in brackets. Although each description is regional, the concept of the genus is broader, with an attempt being made to delimit the group more in terms of all its species. Such an approach is essential, for many genera are represented in our area by only a few outlying species which often belong to different sections or subgenera. Were the viewpoint essentially regional these might be placed in different genera to the obscuring of true interrelationships (and to the ensuing confusion of all). This viewpoint is, in general, a conservative one which stresses similarities, rather than differences. In many instances it would seem far better at this stage of our knowledge to point out a problem than to attempt a solution which may only cause ultimate confusion. The notes included vary widely with the group. Not all branches of botany will be found to be equally well represented: the training and background of the present investigators leads to the emphasis of taxonomic and biosystematic materials, although an attempt has been made to include as much other information as possible. Pathology and palaeobotany, each a large field with its own special and extensive literature, are likely to be represented least well. Limitations of space prohibit the inclusion of the source of each item of information, but a series of selected references will provide many of these. References included are primarily to journals. Many standard texts have been consulted but, rather than to cite each of these repeatedly, it is planned to include a list in the final work. Many references have been annotated as to content, especially when the title is not selfexplanatory. Abbreviations used for journals follow the clear and useful general principles followed by Schwarten and Rickett (Bull. Torrey Bot.

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Club 74: 348–356. 1947, and a much amplified list now in press) which are in accordance with the recommendations of the Madison Botanical Congress of 1893 and the International Code of Botanical Nomenclature, 1956. Those references which we have not seen are followed by an asterisk (*).

The illustrations are by Dorothy H. Marsh (Mrs. Stephen Marsh) who has worked meticulously in depicting the details upon which the accuracy of scientific illustrations depends. Since the adequate illustration of more than a thousand genera is likely to be quite impossible, the drawings have been planned on the assumption that, even though few in number, illustrations which provide some insight into the details of the plant are far more desirable in a work at the generic level than a larger number of "recognition" drawings. These more detailed drawings, which eventually will represent genera scattered throughout the whole range of families, are being made mostly from fresh or preserved materials as these become available. A number of kind individuals have been most helpful in their efforts in this direction, and the living collections of the Arnold Arboretum, which include many woody plants of authentic southern origin, have provided invaluable material. The project is under the direction of Dr. Reed C. Rollins and the writer. Dr. Kenneth A. Wilson is working with us at the present time and we have had as our other excellent collaborators Dr. R. B. Channell, now of Vanderbilt University, and Dr. C. W. James, now of the University of Georgia. All three have worked conscientiously on the many tasks directly concerned with the studies on the Southeastern flora: the preparation of files of references, the identification of specimens, the preparation of generic treatments and the supervision of drawings of groups which they have studied. The basic plan of the generic treatments has been modified through the ideas, trials and efforts of all of us. In these studies a great many friends and colleagues from the staffs of our respective institutions, from many parts of the United States, and from other countries, as well, have brought us appreciated assistance. The appropriate time has not yet come, nor would there be here sufficient space to mention each one individually, but to each I am personally most grateful for his help.

The order Ranales, including as it does the most primitive of known living angiosperms, is one of particular interest from an evolutionary point of view. In recent years, the studies of Professor I. W. Bailey and his numerous collaborators and students have elucidated many aspects of the woody members of this group and have stimulated a renewed interest not only in these plants as a group but in the "complete" approach to problems of the interrelationships of higher categories through the use of information from all parts of the plant, rather than that from a single organ obtained by a single discipline. This approach not only has pointed out the many remarkable primitive structures in various members of this order but has emphasized again and again the very different rates at which structures or organs of a plant may have evolved. Hence, any evolutionary

arrangement of families must be an attempt to sum up the degree of relationship with other groups as well as the over-all level of specialization. The ranalian families included here are those characterized by their predominantly woody habit and by the possession of the characteristic ranalian ethereal oil cells in the tissues of the plant. In our flora this group includes the Magnoliaceae, Annonaceae, Illiciaceae, Schisandraceae, Canellaceae, Calycanthaceae, and Lauraceae. In spite of investigations on these and other ranalian families by numerous authors, a number of families remain to be studied carefully. The interrelationships of all the families of the order are still far from certain, although various related groups have been pointed out. Thus, the Degeneriaceae, Magnoliaceae, Annonaceae, and Himantandraceae form a group of related families within the order; Illiciaceae and Schisandraceae another; Austrobaileyaceae, Trimeniaceae, Amborellaceae, Monimiaceae, Calycanthaceae, Gomortegaceae, Lauraceae, and Hernandiaceae yet another. The relationships of the Canellaceae are undoubtedly with the ranalian complex (presumably with that group of families having monocolpate pollen and tri-lacunar nodes — perhaps Myristicaceae), instead of with the Parietales where they are placed in the Englerian system, but exactly where remains to be seen. I have not attempted to deal at all with the matter of splitting the Ranales (sensu lato) into other orders, retaining all of these families together, instead, and only arranging these groups in this rough way pending the outcome of studies now under way at several institutions.

In connection with these ranalian families Professor I. W. Bailey has given freely and most helpfully of his knowledge of these more primitive angiosperms and Dr. C. E. Kobuski has most kindly read the entire manuscript with a practiced editorial eye. The flowering material used in the illustration of *Illicium floridanum* came through the kindness of Mrs. J. Norman Henry from plants cultivated at the Henry Foundation, Gladwyne, Pennsylvania, and the fruiting specimens through that of Dr. R. B. Channell from Gallman, Mississippi.

MAGNOLIACEAE (MAGNOLIA FAMILY)

Deciduous or evergreen trees or shrubs with simple, alternate, stipulate leaves with pinnate venation, the stipules inclosing the bud and leaving conspicuous encircling scars at each node. Flowers solitary, terminal [or axillary], perfect [except *Kmeria*], all parts free [in ours]. Perianth of 9-15 green, yellow or white tepals in whorls of threes, the outermost whorl sometimes partially differentiated as a "calyx." Stamens numerous, spirally arranged on the elongated receptacle below the carpels, [7-]3(2 or 1)veined, often poorly differentiated into "anther" and "filament" with four microsporangia (often confluent as two), dehiscing longitudinally; pollen ellipsoidal, monocolpate, the germinal furrow distal. Gynoecium of numerous conduplicate carpels, free [in ours], spirally arranged on the upper part of the receptacle and so closely imbricated and packed as to appear JOURNAL OF THE ARNOLD ARBORETUM [vol. XXXIX syncarpous [in ours], the style elongate, vascularized, the ovaries 1-loculed, in both our genera with 2 anatropous 2-integumented ovules at the inner angle of the locule, back to back with the funiculi adjacent. Fruit conelike [in ours], composed of the imbricated follicles or samaras which are clearly distinct at maturity; seeds 2 in each carpel, each with abundant endosperm and a minute embryo; embryo sac development normal in all known cases; basic chromosome-number 19 throughout the family.

A family of about 200 species in 6–10 genera, the generic lines not well agreed upon, but including *Magnolia*, *Talauma*, *Michelia*, *Manglietia* and

Liriodendron. The family is bicentric in distribution: all of the genera occur in eastern or southeastern Asia and Magnolia, Talauma and Liriodendron also occur in the New World. Although many of the 80 fossil "species" of Magnolia and the 25 of Liriodendron are doubtful, the record is sufficient to show that these two genera were formerly of wide distribution in the Northern Hemisphere but have become extinct over most of this area. The family as here considered does not include Schisandra, Kadsura, Illicium, Drimys and its relatives, Trochodendron, Tetracentron, Austrobaileya and other genera which the studies of I. W. Bailey, his collaborators and students have shown clearly to belong elsewhere. Magnoliaceae (sensu stricto) seems to be most closely related to Degeneria and Himantandra. (See also Annonaceae.) Canright notes, ". . . the tissues and organs of the Magnoliaceae reveal many transitions between the more primitive Degeneriaceae and the slightly more specialized Himantandraceae; yet all

three families undoubtedly form a compact alliance within the woody Ranales."

With their woody habit, wood with some primitive features, mostly perfect flowers, numerous and mostly free floral parts with hypogynous and partially spiral insertion, sporophyll-like stamens, monocolpate pollen and ethereal oil cells, the Magnoliaceae are often considered to be among the most primitive living angiosperms. Bailey & Nast in concluding their studies on the Winteraceae (1945) wrote, however, ". . . it is unfortunate that so much attention has been focused upon the Magnoliaceae (sensu stricto) in discussions concerning the origin of the angiosperms, for the seedlings, stems, roots, leaves, stamens, and carpels of these plants all exhibit a relatively high degree of morphological specialization. More primitive and significant ranalian structures are retained by such families as the Winteraceae, Degeneriaceae, Himantandraceae, Trochodendraceae, etc." The detailed studies of Canright bear this out and he concludes, in part, ". . . the evidence in support of the postulated primitiveness of the Magnoliaceae is in some tropical stamen types, plus the occurrence of distalfurrowed monocolpate pollen." It may be added that Sect. Tasmania of Drimys (Winteraceae) appears to combine more numerous primitive features than any other known group of angiosperms. However, in spite of its more advanced position on a world-wide basis, Magnolia is probably the most primitive genus within the Southeastern flora.

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KEY TO THE GENERA OF MAGNOLIACEAE

Leaves entire, acute to cordate-auriculate at the base; petals white, green or yellow; stamens without distinct filaments, introrse or latrorse; styles deciduous; the numerous carpels in fruit forming a cone-like follicetum; carpels opening on the abaxial surface, the seeds pendulous by threads, with a fleshy scarlet to pink outer coat. 1. Magnolia.

Leaves with 4 or 6 lobes, truncate-emarginate at the tip; petals greenish-yellow with an orange band near the base; stamens with distinct, although thick filaments, extrorse; styles persistent, flat and wing-like; the numerous carpels maturing as a cone-like mass of samaras, each of which falls separately. 2. Liriodendron.

Tribe MAGNOLIEAE DC.

1. Magnolia L. Sp. Pl. 1: 535. 1753; Gen. Pl. ed. 5. 240. 1754.

Trees, or sometimes shrubs, mostly with showy and large flowers, the leaves deciduous to evergreen, entire or sometimes cordate-auriculate at the base. Tepals 9–15, in series of 3, white or green to yellow [pink or purple], similar or the outer 3 sometimes partially differentiated, deciduous. Stamens with filament and connective hardly differentiated, the latter produced into a blunt point [in ours] beyond the anther-sace (sporangia); anther-saces 4, linear, opening introrsely or latrorsely. Styles recurved, deciduous, the stigma along the inner face. Fruit a cone-like follicetum of the more or less fleshy imbricated carpels, the individual follicles at maturity clearly separate, dehiscent along the outer (abaxial side), the two seeds hanging by a delicate silky thread of unrolled spiral vessels (from the funiculus and placenta); seeds with a fleshy scarlet to pink outer layer and a hard bony inner layer, both derived from the outer integument. 2n = 38, 76, 114. (Including *Tulipastrum* Spach.) Type species: *M. virginiana* L. (Named in honor of Pierre Magnol, 1638–1715, Professor

1958] WOOD, GENERA OF WOODY RANALES 303 of Botany at the botanical garden at Montpellier, France.) — MAGNOLIA, BAY, CUCUMBER-TREE.

An ancient genus with about 75–80 species, in two centers: about 50 in the Old World (Japan to the eastern Himalayas, south to Java) and about 25 in the New World (eastern U.S., the Greater Antilles, and Mexico to southeastern Venezuela). Dandy divides the genus into 2 subgenera and 11 sections; both subgenera and 4 sections are represented by the 8 species, including 5 varieties, of our area.

Subgenus MAGNOLIA. Anthers dehiscing introrsely; flowers neither precocious nor with a much reduced outer whorl of tepals; leaves evergreen or deciduous. Eight sections, 5 entirely Asiatic, 2 entirely American.

Sect. RYTIDOSPERMUM Spach includes 3 species of Asia and 4-6 of America, all white-flowered and deciduous, with the leaves crowded together near the tips of the branches. *Magnolia tripetala* L., *M. Fraseri* Walt., *M. pyramidata* Bartr., *M. macrophylla* Michx. and *M. Ashei* Weatherby represent this group in our area. *Magnolia macrophylla* and *M. Ashei* are very similar, differing principally in size of plant and shape of fruit, and probably are only varietally distinct. It is also notable that the Mexican *Magnolia dealbata* Zucc., of the mountains of Veracruz to Oaxaca, is hardly distinguishable from *M. macrophylla* and may well be only disjunct populations of that species. All of the species of the section, except *M. pyramidata* and the Mexican plant (as yet uncounted), have

been determined to be diploid (2n = 38).

Sect. MAGNOLIA (*Magnoliastrum* DC.) includes only *M. virginiana*, the Sweet Bay, of wide distribution from eastern Massachusetts to southernmost Florida, eastern Texas and Arkansas. The species, a diploid (2n = 38), is notable for the adnate stipules, leaves glaucous beneath, and very fragrant, small white flowers. Two geographical varieties (var. *virginiana* and var. *australis* Sarg.), based primarily on size of plant and pubescence of branchlets, peduncles and leaves, are currently recognized but need further study.

Sect. THEORHODON Spach is composed of about 15 American evergreen species with stipules free from the petioles. All are tropical in distribution, with the exception of the exceedingly handsome M. grandiflora (2n = 114)which ranges from southern Florida northward on the coastal plain to eastern North Carolina and eastern Texas and Arkansas. Magnolia grandiflora is widely cultivated throughout our region and has escaped in some areas; the exact limits of its native occurrence need to be determined more carefully. Its closest relationships seem to be with the group of species which includes M. Schiediana Schlecht., also with 114 chromosomes, and others of Central America southward to the isolated table-top mountains of southeastern Venezuela. The 8 species of Cuba, Hispaniola and Puerto Rico are all closely related, on the other hand, and form a separate subsection. Magnolia Hamori Howard, of Hispaniola, is a diploid; other chromosome numbers are unknown. 304 JOURNAL OF THE ARNOLD ARBORETUM [VOL. XXXIX

Subgenus PLEUROCHASMA Dandy. Anthers dehiscing laterally or sublaterally; flowers precocious and/or with a much reduced (calyx-like) outer whorl of tepals; leaves deciduous. Three sections, two entirely Asiatic.

Sect. TULIPASTRUM (Spach) Reichb., with the outer whorl of tepals reduced to a small "calyx," includes only the green- or yellow-flowered M. acuminata L. (sensu lato), of eastern North America, and the purpleflowered M. liliflora Desrouss., of eastern China. Both are tetraploids, 2n = 76. Magnolia acuminata, the most variable of our species, appears to be composed of three more or less well defined geographical varieties (var. acuminata, var. cordata (Michx.) Sarg., and var. ozarkensis Ashe), but some aspects of its variation deserve further study. (See Hardin.) No wild hybrids have been found in the genus, although garden hybrids are common. No hybrids between subgenera have been obtained but a number of intersectional hybrids are known, including $M. \times Thompsoni$ ana (Loud.) C. de Vos (M. tripetala \times virginiana) and M. virginiana \times grandiflora. The best known hybrid is the intersectional $M. \times Soulangiana$ Soulange-Bodin (M. denudata \times liliflora) (2n = 95, 114), which is widely grown in a number of cultivars. All species appear to be proterogynous, the stigmas being receptive just before the flowers open. Although Magnolia retains relatively primitive sporophyll-like stamens, especially in some of the tropical Asiatic species of Sect. Gwillimia, the genus is advanced within the family in respect to carpellary features, being surpassed only by Liriodendron which has both more specialized stamens and carpels. Magnolia is most closely related to Talauma: some of the tropical Asiatic species are so similar in flower that fruit is necessary for proper identification.

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Tribe LIRIODENDREAE Reichb.

2. Liriodendron L. Sp. Pl. 1: 535. 1753; Gen. Pl. ed. 5. 239. 1754, "Liriodendrum."

Large, deciduous trees with long-petioled leaves with conspicuous stipules and very characteristic leaf-blades with 2 lateral lobes near the base (and sometimes 2 smaller above) and 2 at the apex which appears as if cut off abruptly by a broad, shallow notch. Perianth segments 9, deciduous, the 3 outer ones sepaloid, green, glaucous, reflexed, the 6 inner ones in 2 whorls making a campanulate, tulip-like corolla, greenish-yellow, each with an orange band near the base. Stamens numerous (± 30) , the filaments stout, narrowed to the broader, apiculate. extrorse anther. Gynoecium of numerous spirally arranged carpels tightly imbricated into a cone-like column as long as the petals; style elongated, broad, flattened and winglike, constricted to a small, recurved stigmatic crest. Fruit a spindleshaped cone of closely appressed 2-seeded samaras, these falling separately at maturity leaving the persistent receptacle; seeds with a thin, dry, and leathery testa. TYPE SPECIES: L. Tulipifera L. (The name from Greek, lirion, lily or tulip, and dendron, tree, from the tulip-like flowers.) -YELLOW-POPLAR, TULIP-POPLAR, TULIP-TREE.

An ancient genus formerly of wide distribution in the Northern Hemisphere, now reduced to two very similar species, *L. Tulipifera*, of eastern North America, and *L. chinense* (Hemsl.) Sarg., of a small area in central China (parts of Kweichow, Chekiang, Hupeh, Kiangsi, and Wushan Provinces).

Liriodendron Tulipifera (2n = 38), a very handsome and important timber tree, reaches its best development in the rich, hardwood forests of the Appalachians, attaining a maximum height of 200 ft. and a circumference of almost 35 ft. It is distributed from western Massachusetts and southern Vermont to southernmost Ontario, southern Michigan, Indiana, southeastern Missouri, eastern Arkansas, and Louisiana to central Florida.

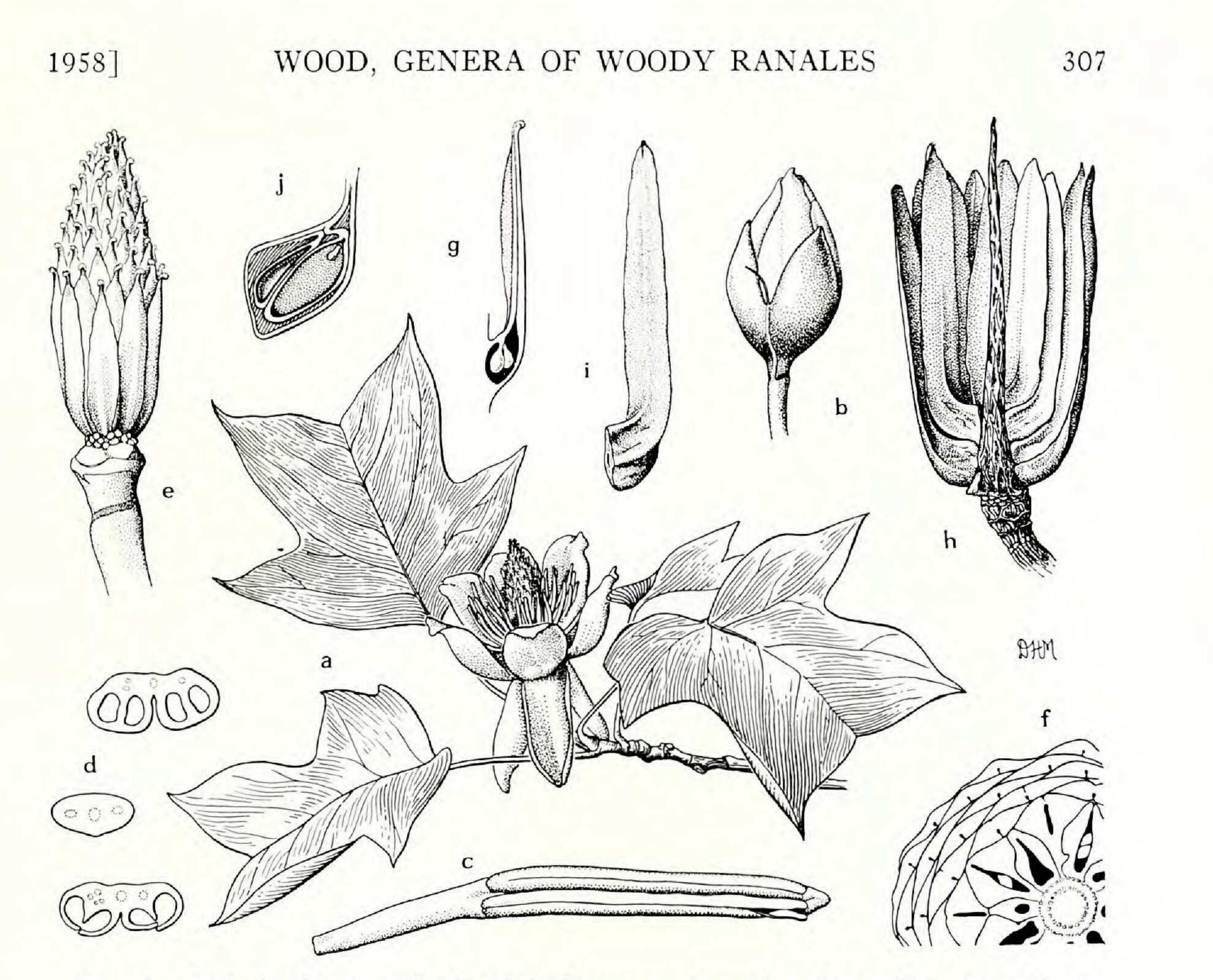


FIG. 1. Liriodendron. a-j, L. Tulipifera: a, flowering branchlet, \times 1/4; b,

flower-bud with stipular bud-scales, $\times 1/2$; c, stamen, abaxial view, $\times 2$; d, unopened anther, filament, and anther after anthesis, cross-sections, pollen omitted, $\times 6$; e, gynoecium, with sepals, petals, and stamens removed, $\times 1$; f, gynoecium, portion of cross-section, with spirally arranged imbricated carpels, ovaries adnate to axis to lower right, increasingly flattened styles toward outside, the locules and stylar canals in black, $\times 3$; g, carpel at anthesis, vertical section, $\times 1$; h, mature gynoecium with many samaras already shed from axis, $\times 1$; i, samara, $\times 1$; j, lower part of samara, vertical section, with aborted ovule (left) and seed with bony coats, abundant endosperm and small embryo, $\times 2$; d, f, g, j, semi-diagrammatic.

The leaves although always unmistakable are extremely variable and most of those described for 25 fossil species may be matched from the existing populations. The faintly fragrant proterogynous flowers of L. *Tulipifera* are provided with copious watery nectar at anthesis, but seem to be visited primarily by bees collecting the abundant pollen. *Liriodendron chinense* (2n = 38) seems to be generally a smaller tree, (ca. 50 ft.) with slightly different leaves, smaller flowers and smaller and slightly different fruit. The plant is not nearly so hardy as our native species. Apparently no crosses between the two species have been made; such hybridizations should be of great interest in view of the geographic isolation of the parental species and in comparison with similar crosses in *Catalpa* and *Platanus*.

Liriodendron is isolated within the Magnoliaceae with no close relatives.

JOURNAL OF THE ARNOLD ARBORETUM VOL. XXXIX 308 It is the only genus in the group with a definitely localized stigma, and the manner of vascularization of the ovules is unique in the family.

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ANNONACEAE (CUSTARD-APPLE FAMILY)

Trees, shrubs [or vines] with alternate, exstipulate, simple, entire leaves with pinnate venation; buds naked, the leaves conduplicate; oil glands present, the plants aromatic. Flowers perfect [in most], hypogynous, regular, axillary [or terminal], usually nodding. Perianth trimerous, generally of 3 small sepals and 6 petals in 2 whorls of 3, the inner smaller [or sometimes lacking]. Stamens numerous, spirally inserted on the receptacle, filament and anther poorly or not at all differentiated, the sterile tip variously modified; sporangia 4, extrorse, opening longitudinally; pollen in tetrads [or single], monocolpate [to acolpate], the germinal furrow proximal. Carpels many-1, usually free but sometimes united by the ovaries at anthesis [and rarely more completely syncarpous]; stigmas terminal; ovules many-1, in 1 or 2 rows along the adaxial wall or basal, anatropous, 2-integumented. Carpels free in fruit and berry-like, or coalescent, forming a fleshy syncarp. Seeds arillate (in ours), with ruminate endosperm and a small embryo. Embryo-sac development normal (Polygonum type) [insofar as investigated], endosperm development cellular.

A tropical family with 75–120 genera and more than 1000 species, many poorly known, and the classification of the family not yet well agreed upon. Represented in our area by Asimina, the only extra-tropical genus, and by Annona, which reaches subtropical Florida.

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The family is distinguished by the exstipulate, simple leaves, the 3 whorls of 3 perianth segments, the numerous more or less fleshy spirally inserted stamens (each with a single vein), the usually numerous carpels, the fleshy fruits, the large seeds with ruminate endosperm, the tri-lacunar nodes with tripartite median trace, and the monocolpate (or derived) pollen with proximal germinal area (evident in those species in which the pollen is shed in tetrads). Anatomical features of wood, stem and leaf are remarkably uniform throughout the family.

It has been agreed generally that the affinities of the group are with the Ranales (sensu lato) but more precise relationships have been a matter of speculation. The anatomical evidence brought together by Vander Wyk and Canright strongly supports the view that the Annonaceae should be most closely allied with Degeneriaceae, Magnoliaceae and Himantandraceae, on a level of specialization above the Magnoliaceae and perhaps roughly comparable with Himantandraceae.

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1. Asimina Adans. Fam. Pl. 2: 365. 1763.

Trees (to 40 ft.), shrubs or subshrubs (ca. 2 ft.). Flowers nodding, axillary on greatly reduced branches, solitary or in pairs, borne on the wood of the preceding season or on the growth of the year, ill-scented or fragrant. Sepals 3 (rarely 4), small, valvate in the bud. Petals usually 6(-8 or sometimes 12), in 2 (or more) series of 3, the outer largest (often very much larger), imbricated, brown or purplish, greenish, white or yellowish, often increasing greatly in size during anthesis. Stamens numerous-10, inserted on the subglobose to nearly flat receptacle; pollen in tetrads. Carpels 15-1, distinct, the styles short, the stigma small; ovules many-6, in two rows or one. Carpels berry-like in fruit (usually one 1-4 maturing) free, banana-shaped or somewhat torulose to ellipsoid or ovoid, the flesh aromatic; seeds flattened to round, many-4, inclosed in a pulpy membranaceous aril. (Including Pityothamnus Small and Deeringothamnus Small.) TYPE SPECIES: A. triloba (L.) Dunal. (The name from asiminier, an early French-colonial name for A. triloba, this, in turn, from the Indian name assimin). — PAWPAW.

Perhaps 10 species, all of eastern North America. Asimina triloba (northern Florida to Texas, north to New Jersey, western New York, southern Ontario, Michigan, Illinois, southeastern Iowa and southeastern Nebraska) and A. parviflora (Michx.) Dunal (Piedmont and Coastal Plain, northern Florida to Mississippi, north to southeastern Virginia) have the widest ranges; the others are mostly confined to Florida. The genus includes the only truly extra-tropical species in the family. According to Fries, the only close relative is Stenanona Standl., of Panama and Costa Rica.

Although the species of Asimina range from deciduous trees reaching 40 ft. (A. triloba) to low, fusiform-rooted shrubs with dimorphic stems and partly persistent leaves and, although there is considerable diversity in flower-color and petal-shape, -size, and -sculpturing, the group appears to be a natural one. The differences used by Small in segregating *Pityo-thamnus* and *Deeringothamnus* seem trivial as generic distinctions. The chromosome-numbers of species of the former group are the same as those of A. triloba and A. parviflora (2n = 18) and, even more significantly, vigorous hybrids have been obtained between A. triloba and at least "A.

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obovata" (= A. grandiflora (Bartr.) Dunal?) and "A. angustifolia" (= A. pygmaea (Bartr.) Dunal?), two very different species assigned to Pityothamnus. The former hybrid is known to be fully fertile. No such data are available for the two species placed in Deeringothamnus (A. pulchella (Small) Rehd. & Dayton, of sw. Florida, and A. Rugelii Robins., of ne. Florida). Although differing in the nearly flat receptacle (correlated with reduced numbers of stamens and carpels), in the narrow, hardly fleshy petals of nearly equal size, and in the lack of bracts on the peduncles of the flowers, these plants appear to be only the most specialized members of the genus, standing at the opposite extreme from A. triloba but connected to it through the "Pityothamnus" group. Although apparently rather stable in its vegetative and floral morphology, A. triloba shows a wide variation in size, color and palatability of fruits. Two general types have been observed: (1) large, yellow-fleshed, highly flavored, early ripening and (2) small to large, white-fleshed, mildflavored, late or very late ripening fruits. A number of selected clones, propagated by grafting, are in cultivation. The flowers of all species are proterogynous. The brown or purple flowers of A. triloba and A. parviflora are reputed to be ill-scented, while those of the white-flowered species, especially A. pulchella and A. Rugelii, are fragrant. Beetles appear to be involved in pollination. Most species set few fruit; hand-pollination seems to be necessary to obtain a good fruit-set in A. triloba.

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- 2. Annona L. Sp. Pl. 1: 536. 1753; Gen. Pl. ed. 5. 241. 1754.

Trees (deciduous with us) with rather coriaceous 2-ranked leaves, nodding flowers borne on axillary or supra-axillary branches (which may abort producing the effect of either terminal or axillary flowers), and fleshy syncarpous fruits. Sepals small, valvate in the bud; petals rather thick and fleshy, generally whitish or yellowish, the outer whorl larger and alternate with the sepals and valvate, the inner smaller or very much reduced [or lacking] and valvate [or imbricate]. Stamens club-shaped, the tip modified, generally broad and truncate, very numerous and tightly packed, inserted on the hemispherical receptacle; pollen grains in columns of tetrads. Carpels sessile, numerous, on the receptacle, the ovaries free or united at anthesis, the styles generally club-shaped, fleshy, and conspicuous; ovules solitary in each ovary (rarely 2), erect. Carpels coalescent, forming a many-seeded syncarp with a smooth, squamulose or muricate surface, the individual carpels being indicated on the surface by more or less distinctly outlined areoles. Seeds ovate or elliptical, with a thin outer coat and a thin aril. TYPE SPECIES: A. muricata L. (The name from anon or hanon, the native Hispaniolan name for A. muricata, but changed by Linnaeus to Latin annona, a year's harvest, in preference to the use of a "barbarous" name, but so that the sound might be kept.) — CUSTARD-APPLE.

A genus of about 110 species assigned to 17 sections, most species tropical American, but about 10 in Africa; several species widely culti-

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vated and naturalized in tropical regions; one species native, one sparingly naturalized and several cultivated in subtropical Florida.

Sect. PHELLOXVLON Saff., with ovate petals, the inner valvate, and ovaries connate at anthesis, includes only Annona glabra L. (2n = 28), the most widespread species in the genus (West Indies, north to the Bahamas and southern Florida, south to southern Brazil, Mexico to Equador; also in Africa from Senegal to the Belgian Congo). Always at low altitudes and associated with abundant moisture, the Pond-apple or Alligator-apple occurs in Florida in the Everglades and coastal areas in shallow ponds,

along the borders of small fresh-water streams or on swampy hummocks; in other areas it seems sometimes to be associated with mangroves. The leaves appear in March–April and flowers in April; the edible but not very palatable fruits ripen in November.

Sect. ANNONA, cauliflorous, but also with ovate petals, the inner imbricate, and with free ovaries, is represented in cultivation by *A. muricata* L., the Guanabana or Sour-sop, a favorite tropical fruit only precariously hardy in Florida.

Sect. ATTA Mart., with elongate petals, the inner greatly reduced, includes A. squamosa L. (Sweet-sop or Sugar-apple), A. reticulata L. (Bullock's Heart) and A. Cherimola Mill. (Cherimoya), all in cultivation in tropical Florida, the first naturalized on some of the Florida Keys.

All species are proterogynous. At the time of pollination a sticky fluid exudes from the stigmas, gluing the styles together and providing a receptive medium for the pollen. The members of sect. Atta seem to be cross pollinated (by beetles?) but A. muricata may be self-pollinated, at least in some areas. Artificial hybrids have been obtained at least between A. squamosa, A. reticulata, and A. Cherimola, and between these species and A. glabra. The Atemoya (A. squamosa \times Cherimola) is regarded as a very promising tropical fruit combining the better features of both parents. The chromosome numbers of the 4 cultivated species above have been reported as both 14 and 16. Numerous cultivars, perhaps involving hybridization, are known in various areas of the tropics. Other species are being introduced and tested for their horticultural possibilities.

According to Fries the genus is most closely related to the American genera Raimondia, Rollinia and Rolliniopsis.

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ILLICIACEAE (ANISE-TREE FAMILY)

A single genus, Illicium L., of southeastern Asia and southeastern North America. Although often placed near Drimys (Winteraceae) or associated with the Magnoliaceae, its closest relatives are undoubtedly Schisandra and Kadsura with which it shares similar pollen, the ranalian type of ethereal oil cell, cambiform "mucilage" cells in the phloem, unilacunar nodes, and similar cuticles, stomata and chromosomes, a combination of characters unique within the Ranales. The total evidence from morphology, anatomy and cytology suggests the inclusion of these three genera either in a single family or in two closely related families; it further pro316 JOURNAL OF THE ARNOLD ARBORETUM [vol. xxxix

vides a strong obstacle to the association of these genera with either Magnoliaceae or Winteraceae. According to the A. C. Smith, "The three genera will probably be treated by future phylogenists as composing a sub-order of the Ranales, coördinate with suborders composed of the (1) Magnoliaceae, Himantandraceae, and Degeneriaceae, (2) Winteraceae, (3) Trochodendraceae and Tetracentraceae, (4) Eupteleaceae, and other combinations of families . . . not yet sufficiently investigated."

Illicium stands apart from the Schisandraceae in its shrubby or arborescent habit, unmodified receptacle, free stamens, vascularized style, comparatively few carpels in a single whorl, single ovule, fruit a single whorl of follicles, unilacunar nodes with a single trace, pseudo-siphonostelic arrangement of the primary tissues, lack of crystal-bearing sclerenchyma, and a specific combination of primitive and specialized anatomical features in the secondary xylem and phloem.

1. Illicium L. Syst. Nat. ed. 10. 1050. 1759.

Glabrous evergreen shrubs or small trees with thin-coriaceous, exstipulate, entire, alternate or distally clustered leaves, the blades decurrent on the petioles. Flowers solitary or 2 or 3 together in minute glomerules, axillary or sub-terminal and appearing crowded among leaves toward the tips of branchlets, sometimes bracteolate, subtended by several caducous bracts. Flowers perfect, hypogynous, the parts free. Receptacle convex to short-conical, usually concealed by carpel-bases. Perianth segments numerous (12-15 or 21-33 in ours), several seriate. Stamens numerous (6-7 or 30-38, rarely -50, in ours), 1-seriate or 2- or 3-seriate, erect, with fleshy filaments and basifixed 4-sporangiate anthers introrsely dehiscent by longitudinal slits; pollen tricolpate. Carpels 11-15(-20), free, in a single whorl, each composed of a laterally flattened ellipsoid ovary distally attenuate into an acute style; style vascularized, conduplicate, stigmatic along the upper side along all or most of its length; ovary unilocular, with a single anatropous ovule on the adaxial side near the base. Fruit a follicetum of a single whorl of free, spreading follicles 10-18 mm. long, these dehiscing along the upper side. Seed with a sub-basal hilum, ellipsoid and laterally flattened, 5-7 mm. long, brownish, glossy; endosperm copious, oily; embryo minute, near the hilum. TYPE SPECIES: I. anisatum L. (The name Latin, illicium, an allurement, in reference to the fragrance of the fruits of I. verum Hook f., an economically important species confused by Linnaeus and others with I. anisatum.) — ANISE-TREE.

A genus of some 37 species of southeastern Asia and 5 of southeastern North America. Two species, representing each of the 2 sections, occur entirely within our area. Our species are easily recognized by the fragrant (when crushed), thin-coriaceous, more or less evergreen leaves, the red to yellow relatively small flowers with numerous perianth segments, and the very characteristic star-shaped fruit, a ring of follicles. Section ILLICIUM (*Badiana* Spach), with 13 species in which the inner

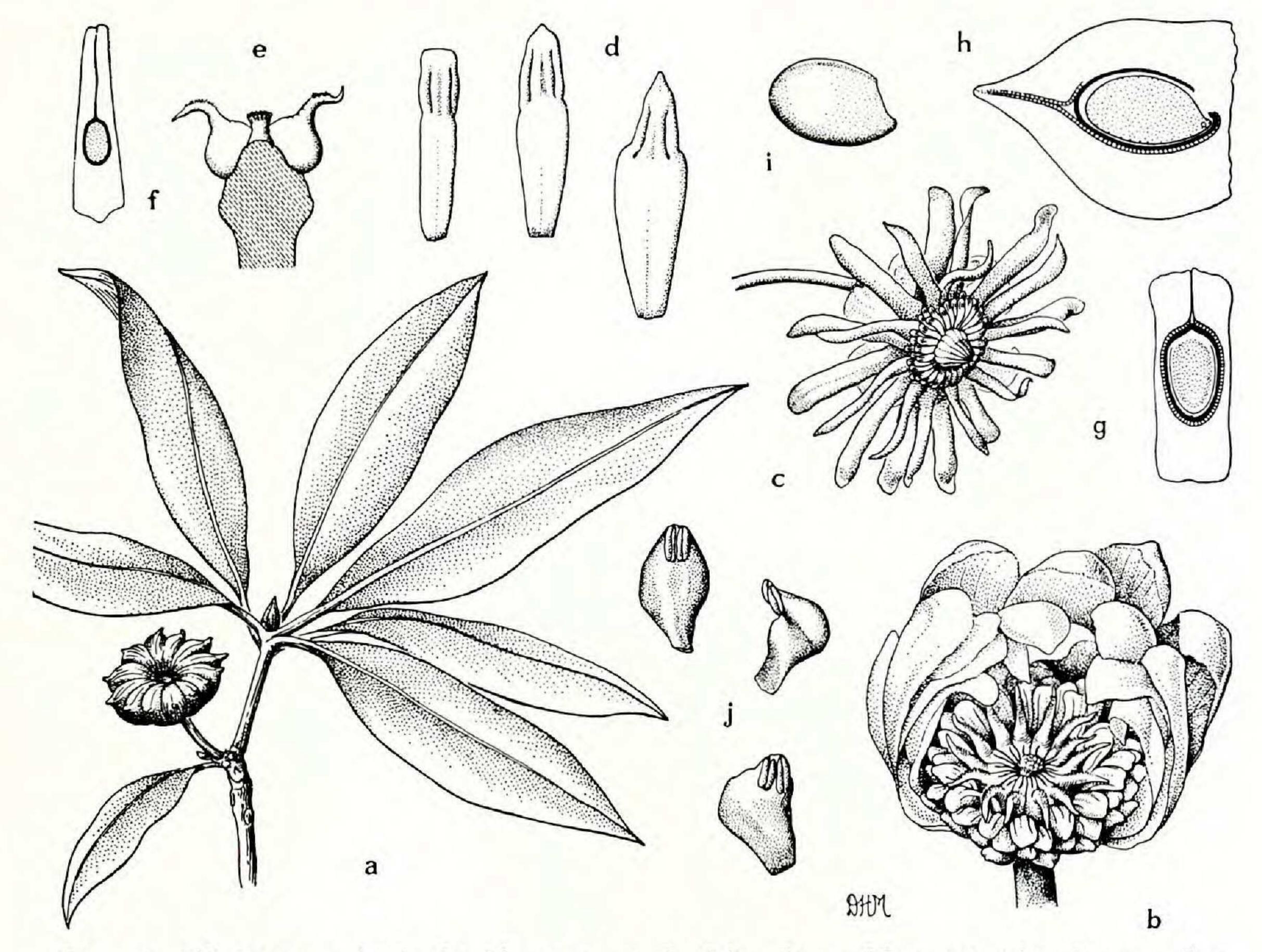


FIG. 2. Illicium. a-i, I. floridanum: a, fruiting branchlet, $\times 1/3$; b, opening bud with carpels receptive to pollen, $\times 3$; c, flower, later stage at shedding of

pollen, the carpels connivent, $\times 1$; d, stamens, inner, outer, and an unusual sub-tepaloid form, adaxial views, $\times 5$; e, two carpels on axis, other flower parts removed, $\times 3$; f, carpel, vertical section, to show folded, unfused sporophyll with single ovule, $\times 10$; g, mature carpel, in section, with horny endocarp (striped) and seed with horny outer seed-coat (black) and endosperm (dotted), $\times 2$; h, mature carpel, cross-section, the mature embryo at micropylar end of seed (to right), $\times 2$; i, seed, $\times 2$; f, g, h, semi-diagrammatic. j, *I. parviflorum*: stamens, adaxial view, $\times 5$.

perianth segments are thin, narrowly oblong or ligulate or lanceolate and somewhat lax at anthesis, is represented with us by *I. floridanum* Ellis (2n = 28), a very well marked species which ranges from northwestern Florida to eastern Louisiana and northward to central Alabama at low elevations, especially in wet areas (e.g., around bay-heads). The only close relative of this species is the very similar and perhaps conspecific *I. mexicanum* A. C. Smith, of Veracruz and Tamaulipas. Both plants differ

from Old World members of the section in their comparatively long pedicels, numerous stamens and brightly colored perianth segments.

The proterogynous flowers of *I. floridanum*, borne from March to May, are showy, deep red or purple, with an intensely unpleasant odor, both features suggestive of pollination by carrion flies. The species is hardy as far north as Philadelphia where, however, it may lose its usually evergreen habit. The leaves were used with those of *Ilex Cassine* as a tea by the Indians of western Florida.

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Section CYMBOSTEMON (Spach) A. C. Smith, with 29 species in which the inner perianth segments are fleshy to paper-like, usually ovate to suborbicular and not lax at anthesis, occurs in our area as I. parviflorum Michx. ex Vent., a shrub or small tree which appears to be restricted to a few counties (Lake, Marion, Seminole and Volusia) at the headwaters of the St. Johns River in northeastern Florida. With its obtuse leaves, small, yellowish flowers produced in May and June and reduced number of stamens (6 or 7), this species is unlikely to be confused with I. floridanum. Beyond our area the section is represented in the New World by I. cubense A. C. Smith, of eastern Cuba, and I. Ekmanii A. C. Smith, of western Hispaniola.

Illicium verum, Star anise of southeastern China and adjacent Indo-China, provides a volatile oil used as a medicine, a condiment, or in flavoring liqueurs such as absinthe and anisette. The seeds of I. anisatum L. (2n = 28), of Japan, contain a poisonous alkaloid.

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SCHISANDRACEAE (SCHISANDRA FAMILY)

A family of two undoubtedly closely related genera of climbing vines, Schisandra Michx. (ca. 25 species) and Kadsura Kaempf. ex Juss. (ca. 22 species), all of eastern and southeastern Asia and Malaysia, with the exception of a single species of Schisandra in the southeastern United States. The two genera have numerous features in common with Illicium (q.v.) but differ in the scandent habit, unisexual flowers, enlargement of the torus after anthesis, arrangement of the carpels, absence of a vascularized

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style, indehiscent drupe-like carpels, unilacunar nodes with three traces, typically eu-stelic arrangement of the primary vascular tissues, relatively primitive type of secondary xylem and presence of crystal-bearing sclerenchyma. Although the group is of great phylogenetic and phytogeographic interest, its economic importance is restricted to the few Asiatic species which occasionally are cultivated as ornamentals.

1. Schisandra Michx. Fl. Bor.-Am. 2: 218. 1803, nom. cons.

Monoecious or dioecious (?) woody climbing vines, the leaves simple, petiolate, exstipulate, alternate on long-shoots or congested on short-shoots, the blade oblong-elliptic to ovate or lanceolate, pinnate veined, entire to sinuate or remotely undulate-denticulate. Flowers pedicellate, unisexual, solitary in the axils of caducous bracts or foliage leaves near the base of the annual shoots, sometimes subtended by 2 or 3 minute secondary bracts. & flowers: tepals 9-12 [5-20], free, 2- or 3-seriate, all similar, the largest elliptic to obovate, 5-8 mm. long; androecium a sessile flattened fleshy 5-cleft pentagonal shield, consisting of 5 radiating stamens with the connectives fused into the shield, the anther-sacs borne on the lower margins of the anthers; opening longitudinally; [in other species stamens 4-60, variously aggregated; pollen 3- or 6-colpate.] 9 flowers: tepals similar to &; gynoecium consisting of a receptacle distinctly longer than broad (1.5-3 mm. long), and numerous (12-)20-30 [-120], 3-5-seriate carpels; ovary ellipsoid to obovoid, the wall fleshy, with stigmatic crests produced distally into an acute, unvascularized pseudostyle and proximally into an irregularly oblong appendage; ovules 2(-3) superposed or obliquely superposed, attached to the adaxial wall of the carpel above the base. Fruit with a greatly elongated receptacle (2-3 cm. long, 2-3 mm. diameter), the pedicel remaining slender, the receptacle bearing 7-12 carpels spaced on its surface; carpels becoming berries, usually ellipsoid or subglobose, the pericarp red, fleshy; seeds 2, ellipsoid-reniform, more or less rugulose; endosperm copious, oily; embryo small, near the hilum. (Stellandria Brickell, 1803, nom. rejic.) TYPE SPECIES: S. coccinea Michx. = S. glabra (Brickell) Rehder. (The name from Greek schisis, a cleaving, and andros, of a man, in reference to the "fissures" between the anthers.)

About 25 species of eastern Asia (Manchuria southward to northern Indo-China and the Himalayas, Java and Sumatra), a single species, S. glabra in southeastern United States, entirely endemic to our area. Schisandra glabra apparently is a very rare plant, being rather poorly known from few and widely scattered localities mostly on the coastal plain in southeastern South Carolina, Georgia, western Florida, Alabama, Mississippi, eastern Louisiana, eastern Arkansas and western Tennessee. The outer perianth segments of the flowers, which are produced in May or June, are greenish, the inner ones increasingly bright red, the androecium red, and the anther-sacs yellow. The greatly elongated receptacle which bears the red or scarlet fruits (July-August) is especially noteworthy.

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The genus has been divided by A. C. Smith into four sections based primarily on various modifications of the androecium, which in the most primitive section (*Pleiostema*) may be composed of relatively numerous (-60) and essentially free stamens. Our species belongs to section *Schisandra* in which the androecium is highly modified, flattened and shieldlike, composed of five united stamens, and presumably representing one of the end-products of the genus. In addition to *S. glabra*, the section includes *S. repanda* (Sieb. & Zucc.) A. C. Smith, of southern Japan and southern Korea, and *S. bicolor* Cheng, of northwestern Chekiang, China. All three are strikingly similar in characters of perianth-segments, androecium and gynoecium and furnish still another example of the now-familiar pattern of disjunction between eastern Asia and eastern North America.

The chromosome numbers of S. (§ Maximowiczia) chinensis (Turcz.) Baill., S. (§ Pleiostema) sphenanthera Rehder & Wilson, and Kadsura japonica (L.) Dunal have all been reported as 2n = 28.

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CANELLACEAE (WILD CINNAMON FAMILY)

A small family of disjunct distribution with five genera of the West Indies, Venezuela, Brazil, East Africa, and Madagascar. The family is notable for the combination of alternate, exstipulate leaves vascularized by 3 traces from 3 gaps, ethereal oil cells throughout the plant, wood with a number of primitive anatomical features, 3 sepals, 4–12 petals in one or more whorls, a monadelphous androecium forming a tube around the ovary with the anthers extrorse, a single pistil with 2–6 parietal placentae, and monocolpate pollen. Although placed in the Parietales in the Englerian system, the relationships to the woody Ranales have been pointed out a number of times. Within that group an affinity to Myristicaceae has been

suggested by several investigators. The family has also been placed by itself in the order Canellales near the Laurales (here included in the woody Ranales).

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- 1. Canella P. Br. Hist. Jamaica 275. pl. 27. fig. 3. 1756; Swartz, Trans. Linn. Soc. 1: 96. 1791, nom. cons.¹

Small tree, to 8–10 m. with gray bark and obovate to oblanceolate, rounded or emarginate, deep green, lustrous, evergreen leaves. Flowers small, perfect, regular, in terminal and axillary cymose inflorescences. Sepals 3, imbricate, persistent, the petals 5, deep red, connate at the base. Stamens 10, completely united in a tube with the 10 linear extrorse anthers on its outer surface below the summit. Ovary superior, 1-locular with 2 parietal placentae and about 4 semi-anatropous ovules, the stigma 2–3 lobed. Fruit berry-like, red, with 2–4 shining black seeds. Embryo small with a large amount of endosperm. Pollen monocolpate. (Winterana L., 1759, nom. rejic.) TYPE SPECIES: Canella alba Murr. (= C. Winterana (L.) Gaertn.). (Name from Low Latin, canella, cinnamon, from Latin,

¹ Conservation unnecessary.

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canna, a cane or reed, applied to the bark which assumed the form of a roll or quill in drying, the name given by Browne to the West Indian plant "the Canella alba of the shops.") — WILD CINNAMON, CINNAMON-BARK.

Probably a single species wide-ranging in the West Indies and with outlying stations in northern South America and in the region of Cape Sable and the Florida Keys, in subtropical Florida, where the plant occurs in hammocks with other tropical genera, generally in the shade of larger trees.

Oil cells are conspicuous in most parts of the plant and the pale inner bark has a cinnamon-like odor. It has been used as a spice, stimulant and tonic. The wood is hard and very dense. The maroon flowers, glaucous on the outside, are borne primarily in June and July (January?) and the crimson fruit matures from March to April. The ripe fruit is eaten by birds which probably disperse the plant. It is cultivated as an ornamental to a limited degree.

The stamens are so closely united that the 10 anthers appear to be a ring of 20 close-packed anther-sacs, each splitting longitudinally. However, ten vascular bundles are present in the tube composed of the filaments.

The genus stands apart in the family by the 10 stamens and the 5 petals coherent only at the base.

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CALYCANTHACEAE (CALYCANTHUS FAMILY).

Shrubs with opposite, entire, exstipulate leaves, numerous strap-shaped tepals spirally arranged on a cup-shaped receptacle, the stamens at its apex and extrorse and the carpels numerous, free, on the inner surface of the receptacle, the mature receptacle resembling a large, dry rose-hip; embryo large, the cotyledons convolute, endosperm lacking.

A small family of disjunct distribution including only two very similar genera (sometimes combined): *Calycanthus* L. (about 4 species of the eastern and western U. S.) and *Chimonanthus* Lindl. (2 or 3 species of China).

The group is notable not only for its odd floral structure (highly modified receptacle and numerous free tepals, stamens and carpels) but for a number of anatomical features, including ethereal oil cells, dicolpate pollen (a modification of the monocolpate type), unilacunar nodes with a fundamentally double trace from a single gap, and 4 cortical vascular bundles (with inverted orientation of xylem and phloem) which extend throughout the stems of mature plants and which have branches entering the leaves at the nodes.

Although some authors have placed the family in the Rosales, the total evidence available clearly indicates that its relationships are with the Ranales, especially that group of families characterized by monocolpate and derived types of pollen and double-trace unilacunar nodes (or unilacunar modifications): Austrobaileyaceae, Amborellaceae, Trimeniaceae, Monimiaceae, Gomortegaceae, Lauraceae, Hernandiaceae, Chloranthaceae, and Lactoridaceae. Its closest relationships are probably with the Monimiaceae, a tropical group, chiefly of the southern hemisphere.

1. Calycanthus L. Syst. Nat. ed. 10. 2: 1066. 1759, nom. cons.

Deciduous shrubs with opposite, entire, exstipulate leaves and red-brown, purple-brown or greenish solitary flowers terminal on short, leafy axillary branches of the season. Receptacle cup-shaped, bearing on its outer surface and apex bracts and numerous undifferentiated strap-shaped, free, rather fleshy tepals. Stamens numerous, on the edge of the receptacle, with stout filaments, the apex of the connective prolonged, succulent, the anthers extrorse; inner stamens reduced to staminodia; pollen 2-colpate. Gynoecium of numerous free carpels within the receptacle; style filiform, stigma terminal, the ovary 1-celled with 2 anatropous, 2-integumented ovules. Fruit an indehiscent pseudocarp from the accrescent receptacle and tepalbases, somewhat resembling a large dry rose-hip, bearing within it the numerous large achenes with tough exocarp. Seed solitary, large, lacking endosperm, the embryo large, with convolute cotyledons. 2n = 22. (Butneria Duham., 1755, nom. rejic.) TYPE SPECIES: C. floridus L. (The name from Greek, calyx, a cup, and anthos, flower.) — STRAWBERRY BUSH, Sweet-shrub, Bubby blossom, Sweet bubby, Sweet bettie, Spicebush.

Perhaps three species of the eastern United States and a single well marked, less closely related species, *C. occidentalis* Hook. & Arn., of the North Coast Ranges and Sierra Nevada foothills of California. The 2 or 3 species of the Asiatic *Chimonanthus*, in which the number of stamens is reduced to five, are sometimes included in *Calycanthus* as a separate section. *Calycanthus fertilis* Walt., *C. floridus* L., and *C. Mohrii* (Small) Pollard are generally recognized in our area, but the range of variation and the true limits of the species are not well understood. Fruit characteristics have been little used but may provide good taxonomic characters.

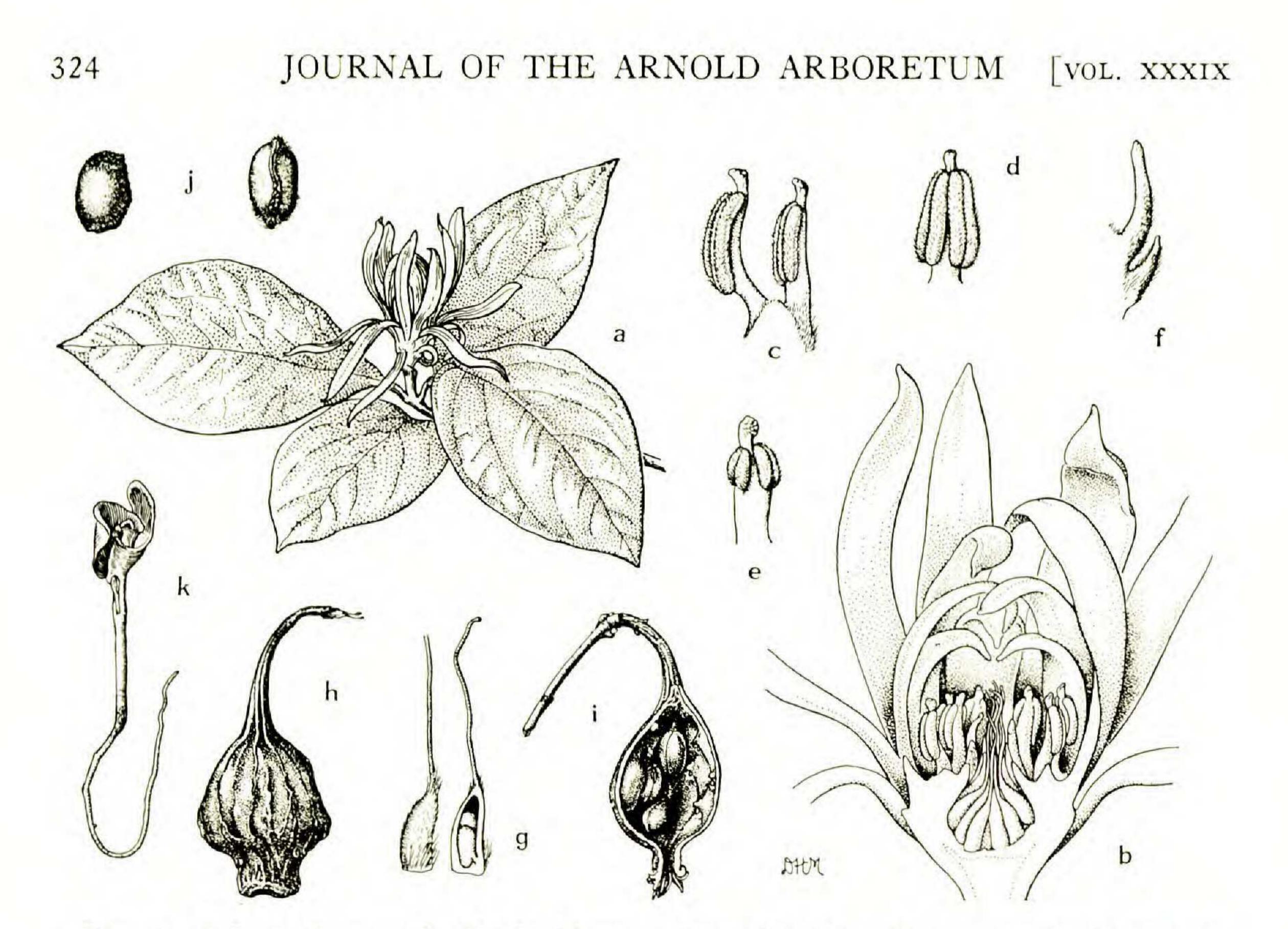


FIG. 3. Calycanthus. a-h, C. floridus: a, flowering branchlet, $\times 1/2$; b, flower, vertical section, to show carpels, stamens, staminodia, and cup-shaped "receptacle," $\times 2$; c, two stamens, lateral view, $\times 5$; d, stamen, abaxial view, $\times 5$; e, inner, reduced stamen, abaxial view, $\times 5$; f, two staminodia from edge of cup, lateral view, $\times 5$; g, carpels, $\times 5$; h, mature dry pendulous pseudocarp,

 \times 1/2; b, g, semi-diagrammatic. i-k, C. fertilis: i, pseudocarp, vertical section, with mature carpels, some removed, \times 1/2; j, mature carpels, lateral and abaxial views, \times 1; k, seedling with unfurling cotyledons, \times 1/2.

Agamospermy (which may account for some of the taxonomic difficulties) has been reported in *Calycanthus fertilis*, *C. floridus*, *C. occidentalis* and *Chimonanthus praecox*. Embryos seem to be of nucellar origin, although parthenogenesis has been claimed for the same species. Pseudogamy appears to be the rule, pollination being necessary for the development of the endosperm, without which the embryo does not grow. *Calycanthus floridus* var. *ovatus* (Ait.) DC., presumably of garden origin, has been reported to be a triploid (2n = 33), with about 50 per cent sterile pollen.

The flowers are proterogynous. Pollination in *Calycanthus occidentalis* has been shown to occur through the agency of *Colopterus truncatus* (Randall), a small nitidulid beetle.

Ethereal oil cells occur especially in bark, leaves, and tepals. The flowers are quite variable in fragrance but some forms have an extremely pleasant spicy, strawberry-like odor when crushed. The seeds contain an alkaloid, calycanthine, with a physiological action similar to strychnine; poisoning of cattle and sheep eating the fruits has been reported in Tennessee.

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LAURACEAE (LAUREL FAMILY)

Evergreen (mostly) or deciduous trees or shrubs with alternate [or sometimes opposite or subopposite], exstipulate, entire or rarely lobed, pinnately veined, subtripli-veined [tripli-veined or 3-veined] leaves, (except Cassytha, a greatly reduced parasite resembling Cuscuta); wood and leaves usually with ethereal oil cells and often with mucilage cells. Inflorescences usually axillary, basically cymose, paniculate or reduced and sub-umbellate, racemose, spicate [or capitate]. Flowers bisexual or unisexual (the plants then dioecious or polygamo-dioecious), small, regular, generally whitish or yellowish, often hairy. Perianth regular, of 6 tepals in 2 whorls of 3, similar or the outer smaller, free nearly to the base or \pm united to form a perianth tube on which the stamens are inserted. Stamens basically 12, in 4 series of 3, the outermost (series I) opposite the outer whorl of tepals, the succeeding series alternating; any one or more series (in all our genera) reduced to staminodia or altogether lacking and the filaments of one (series III) or more series of fertile stamens flanked by stalked or sessile "glands." Anthers 4- or 2-locular, introrse or extrorse, upwardly dehiscent by 4 or 2 flap-like valves; pollen sticky, the contents of each locule raised upward by the valve, grains non-aperturate, single. Pistil 1, with a single stigma and style and a 1-locular ovary with a single pendulous, anatropous, 2-integumented ovule; ovary free from the perianth tube, although sometimes \pm surrounded by it. Fruit a berry or drupe; perianth lobes persistent [often accrescent] or deciduous in fruit, the perianth tube and pedicel often greatly enlarged to form a cupule subtending the fruit, in a few (e.g., Cassytha) the perianth tube completely surrounding the fruit but free from it. Seed lacking endosperm, the embryo large with fleshy plano-convex cotyledons, a small plumule and radicle; germination usually hypogeal. (Including Cassythaceae.)

A family of perhaps 30–40 genera and about 2500 species, mostly evergreen and primarily of the tropics and warm-temperate areas of both hemispheres, especially Central and South America and southern Asia. Represented with us by about 11 native and 2 more or less naturalized species in 8 genera.

The family is easily recognized by the small, regular, usually 3-merous flowers with their curious 4- or 2-locular stamens dehiscent by as many flap-like valves, the 1-locular ovary with a single pendulous anatropous ovule, the baccate fruit often subtended by a cupule derived from the accrescent perianth tube, and the large embryo without endosperm. Equally well characterized by a unique combination of anatomical characters, the Lauraceae seem to form a well-marked and natural family.

The relationships of the Lauraceae seem to be with that group of the woody Ranales (sensu lato) which have secretory cells, unilacunar nodes

and monocolpate, dicolpate or derived (in this case non-aperturate) pollen grains. The relationships are particularly with Monimiaceae (cf. subfam. Hortonoideae, Atherospermoideae), Hernandiaceae, and Gomortegaceae (note woody habit, non-aperturate pollen grains, stamens with associated staminodes, valvular anthers, unilacunar nodes, simple and exstipulate leaves, related alkaloids).

Although the family is a natural one, the generic (and specific) lines are very difficult in some groups of Lauraceae and may be artificial in many instances. Convergent tendencies may be noted again and again. Strong emphasis has been placed upon the various permutations and combinations possible within the 4 series of stamens and staminodes and upon the 4vs. 2-locular condition of the anthers (although both of the latter are known to occur within some undoubtedly related groups, e.g., Cinnamomum, Sassafras). Other important characteristics include inflorescencetype and the development of the perianth tube and lobes and their condition in fruit (persistent, deciduous, cupules, etc.). Patterns of leaf-venation and cuticle may be useful at the specific level but may vary widely within related groups and similar patterns may occur in completely unrelated species. (As a result, generic determinations of fossil materials based on vegetative characteristics are, at best, dubious.) The four trimerous whorls of stamens in the basic lauraceous flower are designated here as series I-IV (cf. Mez), beginning with the outermost whorl which is opposite the outer tepals. The stamens of series III are usually flanked by nectaries (most often stalked and vascularized) which seem to be staminodial in origin. Series IV, if present at all, is usually staminodial. Perfect flowers throughout the family probably are proterogynous, although observations from living plants seem to have been made only on two species of Persea, in which proterogyny is carried to an extreme (dianthesis). Stamens appear to elongate between the time the stigma is receptive and that at which the pollen is shed. The anther valves open from the base upward, recurving and carrying with them the entire contents of the locules.

Only a few species have been examined cytologically, but in these 12 is the basic chromosome number.

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KEY TO THE GENERA OF LAURACEAE

- A. Foliose trees and shrubs; not parasitic. Subfam. LAUROIDEAE.
 - B. Plants evergreen; inflorescences variously cymose-paniculate, with no involucre at the base; flowers bisexual; anthers of at least one series of stamens (III) extrorse. Tribe PERSEEAE.
 - C. Anthers 4-loculed; fertile stamens 9, the 2 outer series introrse; fruits without cupules or the cupules without evident double margins.
 - D. Staminodia of series IV large, cordate-stipitate; locules of anthers of 2 outer series in 2 planes, one above the other.
 - E. Fruit without a cupule at the base, the not greatly enlarged perianth persistent (or sometimes completely deciduous); leaves pinnately veined, lacking glands in the axils of the main veins beneath; perianth lobes unequal to subequal. 1. Persea.
 E. Fruit with a shallow cupule at the base, the perianth lobes deciduous from the enlarged tube; leaves pinnately or subtripliveined, with conspicuous glands in the axils of the main veins

- F. Inflorescences sub-umbellate, involucrate with 4 or 5 decussate scales; fruits bright red on unswollen or slightly swollen pedicels; shrubs.

G. Anthers 2-loculed; inflorescences nearly sessile; branchlets not evidently zig-zag.
G. Anthers 4-loculed; inflorescences clearly pedicellate; branchlets zig-zag.
A. Parasitic orange to green twining herbs of tropical Florida; leaves reduced

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Subfam. LAUROIDEAE Kosterm.

Tribe Perseeae Mez

1. Persea Miller, Gard. Dict. Abr. ed. 4. 1754, nom. cons.¹

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Evergreen trees and shrubs with chartaceous to coriaceous pinnately veined (usually more or less pubescent) leaves. Inflorescences axillary, peduncled, cymose or rarely sub-umbellate (usually described as paniculate but in ours small, with the exception of P. americana). Flowers bisexual, small. Perianth lobes 6, free nearly to the base, the 3 outer ones usually shorter than the inner ones, hairy and persistent in fruit. Fertile stamens 9, staminodia 3; stamen filaments slender, hairy, the anthers 4-loculed, the bases of the 2 upper locules laterally tangential to the apices of the 2 lower; stamens of series I & II introrse; stamens of series III extrorse (or the 2 upper locules lateral and the lower extrorse), the filaments flanked by 2 glands near the base; series IV sterile, the staminodia stipitate with cordate-sagittate tips. Ovary subglobose, the style slender, usually pubescent. Fruit baccate, small and globose or [in P. americana and relatives] large and fleshy and obovoid to pyriform (often obliquely so), borne on the spreading perianth-lobes and scarcely enlarged pedicel; [perianth lobes occasionally deciduous in fruit in some forms of P. americana]. (Farnesia Heist., 1763, nom. rejic.; incl. Tamala Raf.) TYPE SPECIES: Laurus Persea L. = P. americana Miller. (The name an ancient one used by Theophrastus, transferred by Plumier to one of the tropical American

species of Nectandra and afterward adopted by Linnaeus.)

As usually delimited, a genus primarily of tropical America but reaching south to Chile and northward in our area to Delaware and Arkansas and with a single species P. *indica* (L.) Spreng., in the Canary Islands. Two or three native species occur in our area; P. *americana*, in general cultivation throughout tropical America and an important crop in southern Florida, persists after cultivation and has escaped to hammocks. Kostermans has extended the limits of *Persea* to include a number of Asiatic genera.

Persea Borbonia (L.) Spreng., the red bay, is a handsome tree of the borders of streams and swamps and "bayheads," ranging from Florida to Texas, northward to southern Arkansas and Delaware. A variant, Persea palustris (Raf.) Sarg., distinguished primarily on the basis of pubescence is currently treated as f. pubescens (Pursh) Fern. (2n = 24). A third plant, P. littoralis Small, of coastal dunes of Florida, is a small tree with small leaves mostly obtuse at the apex and smooth beneath. The variation in this group is in need of further study. Persea humilis Nash, scrub bay, is a distinctive shrub or small tree of the Pinus clausa-Ceratiola "scrub" of central Florida. Its habit and habitat, reduced inflorescences, somewhat larger fruits, and small leaves silky with shining golden hairs beneath, are characteristic.

¹ Conservation unnecessary.

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The avocado, Persea americana (2n = 24) introduced into Florida at an early date by the Spaniards and long casually cultivated there, has become an increasingly important fruit crop in southern Florida in the last 40 years. Commercial plantations are concentrated especially in Dade County (about 4/5 of the total crop) but extend about as far north as Cape Canaveral, on the east coast, and Tampa, on the west. Scattered trees of the hardier cultivars may be found considerably farther north, however. A large technical and horticultural literature including much of the information available on the genus has accumulated in connection with the cultivation of this species.

Persea americana is a complex species of very wide distribution in cultivation in tropical America. Its origin presumably lies in Central America and involves the group composed of P. americana, its var. drymifolia (Schlecht. & Cham.) Blake, P. Schiedeana Nees, P. floccosa Mez, P. nubigena L. O. Williams, and others, all of the uplands of this region. At the present time three general groups of cultivars are recognized: West Indian (originally introduced there from Central America by the Spaniards), Guatemalan, and Mexican. The three groups differ in characters of foliage, fruit, time of flowering and ripening of fruits, and hardiness. Persea americana var. drymifolia, of the Mexican uplands, is most intimately involved in the Mexican cultivars which are the important commercial types in California but which are not well adapted to the conditions of tropical Florida, where Guatemalan and West Indian forms grow best. In recent years hybrids between members of the three groups have been made and some of these are quite successful (e.g., the 'BOOTH' cultivars, 'HICKSON,' and 'LULA'). The flowers of avocados are proterogynous and have two periods of opening on successive days (dianthesis), the flowers closing in between. "A" and "B" types are recognized. In the former the stigmas are receptive in the morning; the flowers close by early afternoon to re-open the following afternoon when the pollen is shed. In type "B" cultivars, the first (pistillate) opening occurs in the afternoon and the second the following morning. All of the flowers open on a tree at a given time will be in the same stage: thus self-pollination is virtually impossible and both "A" and "B" cultivars are necessary for cross-pollination, an important consideration in the planting of commercial groves. In a sub-type of the "B" form the first period opening is mostly suppressed, with only a few flowers open in the afternoon and most having only a single fairly long period of opening in the morning when the stigmas appear to be receptive and the pollen is shed. Such trees set very few fruit. Beyond this species, observations on pollination appear to have been made only on P. Skutchii C. Allen, of Costa Rica and Panama, which also shows dianthesis with equal numbers of "A" and "B" plants but with the two periods of anthesis between dawn and late-morning (10-11 A.M.) and late-morning and early afternoon (2-3 Р.м.) on successive days.²

² Since the above was written, it has been possible through the kind hospitality of Mr. and Mrs. George R. Cooley for Dr. K. A. Wilson and the author to make some 332 JOURNAL OF THE ARNOLD ARBORETUM [vol. xxxix

Persea is generally considered to be most closely related to Phoebe Nees, a large genus of the tropics of both hemispheres. These genera are conventionally differentiated on the basis of position of anther-locules and nature of the perianth in fruit. Kostermans would reject the former as a generic criterion and would restrict Asiatic Phoebe to those species with an appressed and indurated perianth. The New World species might be retained partly in Phoebe or assigned to Persea and perhaps Cinnamomum. The same author greatly extends the limits of Persea to include the Asiatic genera Machilus Nees, Nothaphoebe Blume, Alseodaphne Nees, Stemmatodaphne Gamble, and Caryodaphnopsis Airy-Shaw, the first three of which would be retained as subgenera.

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preliminary observations on dianthesis in Persea Borbonia and f. pubescens near Brooksville, Hernando County, Florida. Four plants (one the glabrous form and three the pubescent) which began to flower in late April were observed on several days then and in early May 1958. As in Persea americana and P. Skutchii, dianthesis occurred, with both "A" and "B" types being represented (two of each), but, in contrast to these species, the two periods of anthesis occur in the afternoon. Each of the four plants held to a slightly different schedule, but the first afternoon period commenced about noon and ended between 3 and 4:30 P.M. (Eastern Standard Time). The other period of opening occurred between about 3:30 and 4:45. these flowers remaining open until dark (about 7:30) or after, but those of three plants closing before 8 and those of the fourth before 8:30. Flowers in the staminate (second) anthesis are noticeably less rapid in their final closing response, and a few on "B" plants may overlap the opening of new flowers in the pistillate (first) anthesis. Several large wasps and flies were observed visiting the flowers, along with minute flies, small beetles and ants, all apparently collecting nectar. Plants of Persea humilis seen at 3 р.м. in Highlands County, Florida, on May 4, 1958, showed only closed flowers, but branches of one of these (of the "B" type) placed in a polyethylene bag showed later that afternoon and the following day periods of anthesis which appeared to correspond roughly to those of P. Borbonia.

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- 2. Cinnamomum Trew, Herb. Blackwell. Cent. 4, signature м. t. 354. 1760; Blume, Bijdr. Fl. Nederl. Indië 568. 1825 [1826].

Evergreen trees with [or without] conspicuous buds with imbricate scales, the alternate [or opposite] leaves pinnately veined, subtripli-veined, [tripli-veined, or 3-veined], with [or without] glands in the axils of the veins beneath. Inflorescences paniculate, axillary, with deciduous bracts, produced on the growth of the season. Flowers small, inconspicuous, bisexual [rarely polygamous]. Tepals equal, [persistent or] deciduous from the perianth tube. Fertile stamens 9, the anthers 4 [rarely 2]-loculed; staminodia 3: stamens of series I & II introrse, glandless; stamens of series III flanked by glands at the base of the filament, the anthers [extrorse or] the 2 upper locules laterally extrorse, the lower extrorse; series IV of conspicuous stipitate cordate-tipped glandless staminodes. Stigma discoid or peltate. Perianth tube accrescent in fruit, growing out into a thin cup surrounding the base of the fruit; perianth lobes deciduous from the tube

[or the basal part of the entire lobes persistent on the rim]. Fruit in ours a black, globose drupe. (Including *Camphora* Trew, loc. cit. signature L. t. 347; Nees in Wall. Pl. As. Rar. 2: 61, 72. 1831.) Type species: *Laurus Cinnamomum* L. = *C. zeylanicum* [Garc.] Blume. (The name the Latin transcription of Greek *kinnamomon*, derived, in turn, through Hebrew from the ancient name for cinnamon.) — CINNAMON.

A large genus (100-275 species) of eastern Asia, with the largest number in India, Indo-China, China, and Japan, but also in the Philippines, Indonesia, New Guinea, Polynesia and Australia. No species are currently recognized from the western hemisphere, although Kostermans has suggested that some of the American species currently assigned to Phoebe Nees may well belong to Cinnamomum. Section CAMPHORA (Trew) Meissn., characterized by completely deciduous perianth lobes, conspicuous perulate vegetative buds, and alternate leaves with pinnate venation (rarely 3-veined or tripli-veined) and with glands in the axils of the veins, is represented with us by C. Camphora (L.) Nees and Ebermaier (2n = 24). The wood of this species, native to the warm-temperate and subtropical rain-forest zone of eastern Asia from southern Japan to northern Indo-China but now widely planted in the tropics throughout the world, is the source of camphor, which is removed by distillation. The plant was introduced into Florida as early as 1875 as a shade tree and was later established in large plantations in a not very successful attempt to promote a camphor industry in competition with that of Formosa and Japan. At the present time this handsome evergreen with conspicuous scaly buds, very small glaucous flowers (March-April) and black, globose drupes is cultivated in our area as an ornamental tree and for windbreaks from southern Georgia and Florida to southern Louisiana (also s. Texas and Calif.). It is hardy wherever the temperature does not fall below 15°F and has become naturalized to varying degrees throughout this region.

Section CINNAMOMUM (*Malabathrum* Meissn.), in which the perianth lobes are persistent or absciss above the base (leaving the tube crowned by the truncate lobes), the leaf-buds naked or with obsolete scales, and the leaves opposite or subopposite, 3- or tripli-veined and without glands, occurs only in cultivation in the warmer parts of Florida. *Cinnamomum zeylanicum* (2n = 24), the cinnamon of commerce, is a tender plant in sub-tropical Florida, while *C. Cassia* Blume, of China, is a more hardy species in that area.

The flowers of Cinnamomum are similar to those of Persea and Phoebe

but the perianth tube usually is deeper and grows out to form a thin cup in which the fruit sits. Some species have the anther-locules arranged in an arc (*Neocinnamomum* Liou), a situation paralleled in *Phoebe* vs. *Persea* and *Nectandra* vs. *Ocotea*. Close relationships with *Aiouea* Aubl. and *Phoebe* and also with *Ocotea* have been postulated by Kostermans.

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- 3. Nectandra Rolander ex Rottböll, Acta Lit. Univ. Hafn. 1: 279. 1778, nom. cons.

Trees [and shrubs] with alternate coriaceous [to membranaceous] leaves usually pinnately veined, the reticulation conspicuous [or obscure].

Inflorescences usually paniculate, axillary or subterminal, the narrow bracts deciduous. Flowers bisexual, small, the 6 elliptic perianth lobes hairy, spreading or reflexed at anthesis, deciduous, the tube conspicuous or almost entirely lacking. Fertile stamens 9, the staminodia 3 [when present]: stamens of 2 outer series (I & II) with nearly sessile reniform anthers [or fleshy and petaloid], the anther-locules 4, arranged in an arc, introrse. Stamens of series III longer, the squarish anthers on filaments almost equal their length, with 2 large subreniform nearly sessile glands at the base of filaments, the 4 anther-locules in two horizontal planes, the 2 upper laterally extrorse, the 2 lower extrorse. Staminodia stipiform (in ours triquetrous, on slender pubescent filaments). Ovary glabrous; stigma capitate, conspicuous. Fruit a thin-walled drupe, ellipsoid, globose or oblong, with a shallow woody cupule (formed by the enlarged perianth tube) subtended by the enlarged pedicel; cupule margin simple. (Not Nectandra Berg., 1767.) TYPE SPECIES: N. sanguinea Rol. ex Rottb. (The name from Greek, nektar, nectar, and andros, of a man, in reference to the stamens and anther valves which were mistaken for nectaries and stamens, respectively.) — LANCEWOOD.

A large genus (about 175 sp.) of tropical America, the majority of the species in South America (especially the Andes), with about 35 in Central America, and a few in the West Indies. Nectandra coriacea (Sw.) Griseb. (Ocotea coriacea (Sw.) Britton), which occurs in the West Indies, the Yucatan Peninsula, British Honduras, and Guatemala, reaches southern Florida, where it extends as far north as Indian River County, on the east coast, and Cape Romano (Collier County), on the west. This species, which may reach 30-40 feet in height, bears small panicles of small, white, very fragrant jasmine-scented flowers which are followed by the first green, then dark-blue, then black fruit with green, yellow or red cupule and enlarged fruiting pedicel. Flowering and fruiting are quite variable. The leaf-venation is its most outstanding characteristic: there are 6-8 pairs of lateral nerves which are rather obscured by a very conspicuous over-all elevated reticulum (at least in dried specimens). Nectandra coriacea is most closely related to N. salicifolia (HBK.) Nees (N. sanguinea sensu Nees, non Bol. ex Rottb.), of wide distribution in Mexico and Central America.

Nectandra is distinguished from Ocotea Aubl. (1775) by the arrangement of the anther-locules of the two outer series of stamens, these being in an arc in the former and in two planes in the latter, a distinction which does not entirely hold. Further studies in tropical America may well show that Nectandra should be regarded as a subgenus of Ocotea, a course recently advocated by Kostermans. It has been suggested, on the basis of the illustration of Ocotea Catesbyana in Sargent, Silva 7: pl. 303, that both Nectandra and Ocotea occur in southern Florida. Although this illustration does show the antherlocule arrangement of Ocotea, rather than that of Nectandra, this would appear to be an error, for only Nectandra coriacea (also incorrectly drawn 338 JOURNAL OF THE ARNOLD ARBORETUM [vol. xxxix

in Small's Manual) seems to be represented by herbarium specimens, including those studied by Sargent, from southern Florida. The disposition of Ocotea Catesbyana (at least sensu Sargent) as a synonym of N. coriacea would appear to be the correct one.

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4. Licaria Aubl. Hist. Pl. Guiane Franç. 1: 313. pl. 121. 1775.

Evergreen trees [or shrubs] with pinnately-veined leaves and small flowers in axillary or subterminal panicles near the tips of the branchlets [or flowers rarely solitary, subumbellate or capitate]. Flowers bisexual; tepals 6, in two whorls, [spreading or] erect, united below into a distinct perianth tube; (in ours, flowers obconical, ca. 2-2.5 mm. long, the perianth tube about half this length). Fertile stamens 3: stamens of series I & II [small and staminodial or] abortive; stamens of series III fertile, [entirely free, partly connate or] united into a staminal tube, their anthers 2-loculed, extrorse [or introrse], the filaments each with 2 glands (these in ours flattish, pressed against the staminal tube below the anthers, united in pairs, touching each other); stamens of series IV abortive [or rarely staminodial, minute]. Ovary included in perianth tube, free, the style thick [to slender], stigma inconspicuous. Berry ellipsoid, (in ours black, to 2 cm. long), smooth, the base partly covered by a thick, hemispherical double-margined cupule, the inner margin entire, erect, the outer one spreading, thicker, irregular, the pedicel thickened, merging into the tube. Cotyledons flat-convex, large, including the minute 2-4-leaved, glabrous plumule and minute conical radicle. (Acrodiclidium Nees & Mart. 1833; incl. Misanteca Schlecht. & Cham. 1831, Chanekia Lundell, 1937 and others.) TYPE SPECIES: L. guianensis Aubl. (The name derived from *licari kanali*, the native name of the type species.) — Sweetwood.

A genus of about 45 species of wide distribution in tropical South and Central America and the West Indies; a single species, *L. triandra*, of the West Indies from Martinque to Cuba, has been known from a single locality in our area.

The handsome Licaria triandra (Sw.) Kostermans (Misanteca triandra (Sw.) Mez) is one of the rarest plants in our flora, if it still persists at all. It was first recorded from two trees discovered in 1910 in Brickell Hammock, in Miami, but as many as 25 trees were counted there as recently as 1946 by the late W. M. Buswell (see Little, Checklist of Native and Naturalized Trees of U. S.). However, this unique hammock has been swallowed up and destroyed by the greedy real-estate development of metropolitan Miami and the species is presumably extinct at that locality. Apparently a few trees (planted) still survive on the campus of the University of Miami. Licaria, as used here, includes, among others, Acrodiclidium (characterized by the presence of series I and II as staminodes, the stamens of series III free), Misanteca (in which staminodia are lacking and the stamens of series III united), and Chanekia (lacking staminodia and with stamens free). These genera merge with one another and share their "general facies, the shape of the cupule, ovary and stigma," characters which also separate them from Mezilaurus and Endiandra, their nearest allies (Kostermans). Although there is agreement that the group as now constituted is a natural one, the proper name for it has been a matter of dispute. Licaria is based upon sterile material which Kostermans identifies positively with Acrodiclidium; Lundell, however, rejects Licaria in favor of Misanteca because the genus is based upon a sterile specimen.

Our species falls into subgenus MISANTECA (Schlecht. & Cham.) Kostermans. Apparently L. triandra [West Indies], L. limbosa (Ruiz & Pavon) Kosterm. [Venezuela to Peru and Bolivia], L. Pittieri (Mez) C. Allen [Costa Rica], L. Cervantesii (HBK) Kosterm. [southern Mexico, Guatemala], L. caudata (Lundell) Kosterm. [Br. Honduras, Guatemala], and L. Cufodontisii Kosterm. [Costa Rica] form a group of more or less closely related species.

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Tribe LITSEEAE Mez

5. Sassafras Trew, Herb. Blackwell. Cent. 3, signature P. t. 267. 1757; T. F. L. Nees & Ebermaier, Handb. Med.-Pharm. Bot. 2: 418. 1831.

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Deciduous trees with elliptic leaves, entire, mitten-shaped or 3-lobed at the apex, narrowed at the base, involute in the bud; buds with few imbricate outer scales. Plants usually dioecious, the flowers usually unisexual [or apparently bisexual, but not often functionally so], in lax, drooping, few-flowered "racemes," the upper flowers of the lowest raceme opening first. Perianth of 6 yellowish tepals, in two whorls of 3. Staminate flowers with 9 fertile stamens on the margin of the short perianth tube; anthers 4 [or 2]-loculed, introrse (but the lower locules of series III latrorse), opening by 4 [or 2] valves; filaments flattened, elongated, those of series III with a pair of orange-colored short-stipitate glands at the base; staminodes and pistillode absent [or 3 staminodes and pistillode present in the Asiatic species]. Pistillate flowers with 6 rudimentary stamens, in 2 whorls [or 12 in 4 whorls, similar to stamens and staminodes in staminate flowers]; ovary ovoid, nearly sessile in the short perianth tube, the style slender, the stigma enlarged. Fruit a dark blue ovoid berry supported by the club-shaped enlarged and fleshy pedicel and perianth base. Seed oblong, pointed; testa thin; embryo subglobose, erect. (Including Pseudosassafras Lec., Yushunia Kamikoti.) Type species: Laurus Sassafras L. = S. albidum (Nutt.) C. G. Nees. (The popular name for the plant, used as early as 1569 by the French in Florida, adopted by Trew.)

As currently delimited, a genus of three species of eastern Americaneastern Asiatic distribution: Sassafras albidum (2n = 48) (including var. albidum and the more southern var. molle (Raf.) Fern.), of wide distribution from s. Maine to se. Iowa, s. to Texas and Florida; S. Tzumu (Hemsl.) Hemsl., of central China (from Kwantung and Kweichow, to Szechuan, Hupeh, Anhwei, and Chekiang); and S. randaiense (Hayata) Rehd., of the central mountain range of Formosa. The two Asiatic species constitute the subgenus PSEUDOSASSAFRAS (Lecomte) Keng. Both are less specialized than the American and differ from it in the pubescent tepals, in the presence of 3 staminodes and a pistillode in the staminate flowers, and in having in the pistillate flowers 12 staminodes similar in appearance to the stamens and staminodes of the staminate flower. The anthers of S. Tzumu are 4-loculed, those of S. randaiense 2-loculed. All three plants are similar, however, in habit, bark, winter buds, leaves, inflorescence and fruit and certainly constitute a natural genus (although each of the three has been assigned to a separate monotypic genus at one time or another). Rehder suggested that the nearest relative of Sassafras is Lindera (some of the deciduous species of which have lobed leaves very similar to those of Sassafras) which differs primarily in its 2-celled anthers and in the "umbellate" inflorescence. Kostermans, however, would ally Sassafras with the evergreen Actinodaphne Nees, a rather different group, more suggestive of Litsea.

Sassafras albidum is with us a very familiar plant, long reputed to have medicinal properties. It is at most a mild, aromatic stimulant. Gumbo filé, a powder used to give flavor and consistency to gumbo soup, owes its

properties to the secretory and mucilage cells of the leaves from which it is prepared.

Although seldom planted, the species is one of our most handsome native plants, attractive at all seasons of the year. The tree occasionally reaches a height of 80–90 feet and a diameter of 6 feet. It is sometimes weedy, for it tends to sucker from the roots. The attractive small, yellow flowers are produced in early spring with the first unfolding of the leaves.

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6. Lindera Thunb. Nov. Gen. Pl. 3: 64. 1783; Blume, Mus. Bot. Lugd.-Bat. 1: 323. 1851, nom. cons.

Dioecious or polygamo-dioecious shrubs with entire [or 3-lobed] deciduous [or evergreen] leaves. Flowers small, yellow, short pedicelled, in almost sessile [in ours] umbel-like cymose clusters of 3-6, each cluster subtended by 2 pairs of decussate deciduous bracts, the clusters 1-4 above the axils of the preceding year's leaves on greatly reduced supra-axillary branches terminated by a vegetative bud which grows after anthesis. Tepals glabrous, the two whorls similar, thin, the perianth tube very short or none; perianth deciduous, only a small disc remaining beneath the fruit in ours. Staminate flowers with 9 stamens (series IV completely aborted), the 3 innermost (series III) each with a pair of conspicuous stalked glands at the base; anthers 2-loculate, all introrse; pistillodium present. Pistillate flowers with stamens variously developed, the innermost series usually reduced to filaments with two glands at the base; some staminate flowers sometimes present among the pistillate; ovary and style about equal. Fruit a bright red drupe on the short, hardly or slightly thickened pedicel topped by the disc-like somewhat accrescent perianth base. (Benzoin Fabr. 1763, non Lindera Adans. 1763, nomina rejicienda.) TYPE SPECIES: L. umbellata Thunb. (Named for John Linder, 1676–1723, early Swedish botanist.) — WILD ALLSPICE, SPICEBUSH.

A large genus, of about 100 species, both deciduous and evergreen, primarily of eastern Asia, with only two in the western hemisphere, both occurring in our area. *Lindera Benzoin* (L.) Blume, var. *Benzoin* is widespread along streams and in damp woods from southwestern Maine to southern Michigan and Illinois, south to North Carolina, Kentucky, Missouri and southeastern Kansas. Its var. *pubescens* (Palmer & Steyerm.) Rehd. is more southern in distribution, reaching Florida and Texas. *Lindera melissifolia* (Walt.) Blume is apparently exceedingly rare and local being known from widely scattered localities from Florida to Louisiana, northward to southern Missouri and to eastern North Carolina. The two species are quite distinct, differing in their ecology and in numerous morphological features. (See Steyermark.) Both are known to occur close together but in different habitats in southern Missouri.

Lindera Benzoin is a handsome shrub, worthy of cultivation, although, like most native plants, it is seldom grown. The flowers are among the very earliest to appear in spring. Staminate flowers are somewhat larger than pistillate and frequently occur in clusters of 3 or 4 umbels, in contrast to the less conspicuous pistillate inflorescences which are usually either single or paired. As a result, staminate plants are far more frequent than pistillate in the flowering condition in herbaria. This species and the Asiatic L. praecox and L. glauca have all been reported to have 24 somatic chromosomes.

Characters of flower and fruit in *Lindera* are very similar to those of *Litsea*, the two genera being distinguished primarily by the 2-loculed (or

1958] WOOD, GENERA OF WOODY RANALES 343 very rarely partly 4-loculed) anthers of *Lindera* vs. the 4-loculed anthers of *Litsea*.

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7. Litsea Lam. Encyc. Méthod. Bot. 3: 574. 1791, nom. cons.

Dioecious, [evergreen or] deciduous shrubs with pinnately veined leaves and naked [or imbricate-scaled] buds. Flowers unisexual, in small pedunculate axillary sub-umbellate 3–5 flowered clusters, each with an involucre of 4 or 5 decussate deciduous scales, globose before anthesis; in our species borne singly above the scar of leaves of the preceding year near the tips of the branches, or 2 or 3 on very short axillary branches. Tepals yellow, 6 [or occasionally fewer or lacking], almost completely free [or united into an ovoid or campanulate tube], deciduous after anthesis. Staminate flowers with 9 [or 12] fertile stamens, those of series III [and IV] with 2 stipitate glands at the base; filaments well developed, in ours 2–3 times as long as the ovate emarginate anthers; anthers all 4-locular, all introrse; pistillode lacking [or small]; staminodia none in our species. Pistillate flowers with 9 [or 12] staminodia, those of series I and II usually without glands, those of III [and IV] flanked by 2 glands at the base of the fila-

ments; ovary attenuate into the style, the stigma dilated. Fruit a more or less globular berry seated on a minute disc [or on a shallow cupule or disc on the enlarged pedicel]. (Malapoenna Adans. 1763, Tomex Thunb. 1783, Sebifera Lour. 1790; nomina rejicienda. Glabraria sensu Blume, 1851, not L. = Boschia Korthals [Bombacaceae]). Type species: L. chinensis Lam. = L. sebifera Pers. (according to list of nomina conservanda) or = L. glutinosa (Lour.) C. B. Robinson (according to Kostermans). (The name presumably from a local name of southern China, litsé JOURNAL OF THE ARNOLD ARBORETUM [vol. XXXIX de Chine being given as the common name for the type species.) — POND-SPICE.

A large genus of perhaps 400 species, mostly evergreen, and primarily of eastern and southeastern Asia from Japan to the Philippines, India, New Caledonia, tropical and subtropical Australia and New Zealand, with 5 species in North America. Of the American species, 3 are distinctive closely related plants of the eastern Sierra Madre of Mexico; the fourth, L. glaucescens HBK. is highly variable and widespread from northwestern Mexico east and south to Costa Rica; the fifth, L. aestivalis (L.) Fern. (L. geniculata (Walt.) B. & H.), is a rare plant of very spotty distribution on the coastal plain from Florida to Louisiana, north to eastern North Carolina, southeastern Virginia (at least formerly), and Tennessee, occurring around pond-margins and in swamps. Litsea aestivalis is a shrub to 2 or 3 m. with characteristic zig-zag branchlets and narrowly oblong leaves. The pedunculate and involucrate umbel-like clusters of small yellow flowers are borne in early spring before the appearance of the leaves (this being the only deciduous American species). The bright-red globose fruit is borne in early summer. Like Lindera, presumably a close relative (from which it differs primarily in the 4-loculed anthers), the genus is complex and taxonomically difficult in eastern and southeastern Asia, where the interrelationships of Litsea, Lindera, Sassafras, Actinodaphne, Neolitsea and others are to be sought.

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Subfam. CASSYTHOIDEAE Kosterm.

8. Cassytha L. Sp. Pl. 1: 35. 1753; Gen. Pl. ed. 5. 22. 1754, "Cassyta."

Parasitic green to orange twining plants with wiry chlorophyll-bearing stems and minute, spirally arranged scale-like leaves, the plants superficially resembling *Cuscuta* and attached to host plants by small haustoria. Inflorescences indefinite, spicate [or racemose or reduced to heads], the

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minute flowers borne singly at irregularly separated nodes, sessile [or pedicellate] in the axil of a minute bract, with 2 similar bracteoles close under the perianth, bisexual. Tepals 6, the outer whorl much smaller and resembling the bracts, united below to form a shallow tube to which the stamens are adnate, later accrescent and inclosing the fruit. Fertile stamens 9, 2-loculed, staminodia 3: stamens of series I sub-petaloid, series I & II introrse, without glands; stamens of series III flanked by nearly sessile glands, the anthers extrorse; series IV of distinct cordate sessile [or stipitate] staminodes. Ovary broadly fusiform, the style indistinct, the stigma capitate. Fruit drupaceous with a hard endocarp, completely inclosed by, but free from the enlarged and succulent cream-colored perianth tube which has a small opening at the apex surrounded by the persistent erect perianth lobes. Seed coat membranous or coriaceous; cotyledons thick, fleshy, often unequal, sometimes more or less consolidated at maturity. Type species: C. filiformis L. (The name from Greek, kasytas or kadytas, dodder [Cuscuta].) — WOE-VINE, LOVE-VINE.

A curious genus with perhaps 15–20 species, more or less maritime and mainly Australian but with a few in Africa and a single species, C. filiformis, of pantropical distribution and the only species in the Americas. Cassytha filiformis occurs in the subtropical portions of our area, primarily in coastal areas as far north as Brevard and Pinellas counties, where it may easily be mistaken at first for Cuscuta. It is parasitic on a wide range of herbaceous and woody hosts and can be a destructive pest. Although Cassytha is an obligate parasite, the plant is at least partly autotrophic, for chloroplasts with abundant starch are present in the cortical parenchyma throughout the stem. In addition, numerous stomata (oriented transversely on the stem), an extensive xylem system, and haustoria with many well-developed spiral tracheae running to their ends which curve directly into the wood area of the host, all suggest that the plant is primarily a water-parasite. This habit, the reduction in exposed surface, the extreme development of mucilage in the plant (reminiscent of the cacti), and the profuse development of the plant in the brilliant sunlight of coastal and white-sand scrubs suggest further a special adaptation to a xerophytic type of habitat unfavorable to most Lauraceae. Seedlings germinate in nearly pure sand and elongate quickly with rather rapid nutating movements which bring about contact with a host plant. The primary root remains rudimentary and only four secondary roots (which lack root-caps) function during the period prior to attach-

ment to the host.

Although the inflorescences of Cassytha are described as "indeterminate" racemes or spikes or (in a few species) heads, the "inflorescences" would not seem to be radical departures from the usual determinate, basically cymose inflorescences of other Lauraceae, but would merely reflect the reduction to "simplicity" in this highly modified plant. Each of the solitary axillary flowers with its two minute bracteoles would appear to be the product (by reduction) of an entire cymose lauraceous inflorescence.

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Thus the short "racemes" or "spikes" of *Cassytha* would represent a stem with inflorescences (each reduced to one flower) produced at successive nodes, just as in many Lauraceae a succession of axillary inflorescences is produced as the growth of the season proceeds. The even more highly modified capitate inflorescences of some species of *Cassytha* would be derived through shortening of the internodes of "spicate" inflorescence.

Cassytha is sometimes separated from the Lauraceae on account of its great reduction and parasitic habit but in all anatomical features (including rubiaceous stomata, ethereal oil cells and mucilage cells) and in all floral characters it is very clearly a member of that family. In flower and fruit it approaches Cryptocarya R. Br., a large pantropical genus, in which the fruit is completely inclosed in the enlarged perianth tube.

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